

THE TAXONOMIC RELATIONSHIP BETWEEN *MALACLEMYS* GRAY, 1844 AND *GRAPTEMYS* AGASSIZ, 1857 (TESTUDINES: EMYDIDAE)

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Abstract

The turtle genus *Graptemys* is a distinctive group clearly separable from *Malaclemys* on the basis of external and osteological features. The difference between the groups indicate that the degree of genetic relationship is no closer than that resulting from their both having presumably arisen from a *Pseudemys*-like stock or *Malaclemys* from a *Graptemys* stock.

INTRODUCTION

Investigators of *Malaclemys* and *Graptemys* have based their taxonomic allocations on penial, skull, shell, hind limb and pelvic girdle morphology and on head patterns. Osteological comparisons, when indicated, were usually limited to the skull, and in most cases, head patterns were used to distinguish taxa. The degree of evolutionary conservatism and parallelism exhibited by turtles argues against the use of external characters (e.g., head striping), alone in determining taxonomic and phylogenetic relationships. Thus, both osteological and surficial features have been examined in this study.

HISTORICAL REVIEW

The controversy about the relationship between *Malaclemys* and *Graptemys* began as a result of the lumping of *Graptemys* with *Malaclemys* by Boulenger (1889) and the re-establishment of the genus *Graptemys* by Baur in 1890. Since

that time, W.P. Hay (1904) and O.P. Hay (1908) followed Baur in recognizing the two genera, as did Carr in 1949. Later, however, Carr (1952) questioned the validity of separating the two genera and McDowell (1964), without presenting supporting data, lumped *Graptemys* with *Malaclemys*. Zug (1966, 1971), on the basis of similar penial, pelvic girdle, and hind limb morphology for the two genera considered them congeneric, and Parsons (1960, 1968) found the choanal structures of both genera to be so variable that the evidence did not particularly support or refute the congeneric idea. Several other authors (Ernst and Barbour, 1972; McKown, 1972; Dundee, 1974; Killebrew, 1979; Dobie and Jackson, 1979; Pritchard, 1979; Vogt, 1978, 1980) have not supported the synonymy of *Graptemys* with *Malaclemys*; they evidently must believe that sufficient evidence has not been presented to lump the two genera together.

The purpose of this study is to clarify the generic status of *Malaclemys* and *Graptemys*.

MATERIALS AND METHODS

Representatives of each of the ten extant *Graptemys* species (Vögt, 1980) and their subspecies and individuals of several subspecies of the monotypic *Malaclemys* were examined. External features, includ-

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ng scute contracts, plastral patterns, and striping on the head and leg were analyzed in juvenile and adult turtles of both sexes. Skull and shell characters were analyzed on large sub-adult and adult females. Skull terminology is that of Gaffney (1972 a); scute and bone terminology is that used by Zangerl (1969).

The method used to elucidate the relationship between *Malaclemys* and *Graptemys* and to other North American emydid turtles is the search for taxa that have shared derived characters. This method was described by Hennig (1966), and has been used by others (Gaffney, 1972 b, 1975; W.E. Clark, 1978) and is called phylogenetic systematics or cladism.

DIAGNOSTIC CHARACTERISTICS

The diagnostic characteristics of *Graptemys*, *Malaclemys* and an outgroup comparison of those genera with the other North American emydid genera are listed in Table 1. Each feature is also designated as either ancestral (primitive) or advanced (derived).

SIGNIFICANCE OF DIAGNOSTIC CHARACTERISTICS

The number (s) in a bracket refers to the number of the diagnostic features in Table 1.

SKULL FEATURES

(1) Quadratojugal - maxilla contact. If the absence of contact between these two bones represents the primitive state, then the possession of the derived condition in three *Graptemys* species (in one *pseudogeographica* and in all *pulchra* and *barbouri*), in *M. terrapin*, and in some *Pseudemys* species suggests that *M. terrapin* could have been derived from one of these *Graptemys* or *Pseudemys* species. *Graptemys* could have come from any group lacking contact between the two bones.

(2) Spoon-shaped symphysis of lower jaw

(Fig. 1). The flattened spoon-shaped nature of the symphyseal part of the lower jaw apparently is a derived feature in *Graptemys*. The absence of such a structure in *Malaclemys* suggests that *Graptemys* was not ancestral to *Malaclemys* and that *Malaclemys* may have arisen from some *Pseudemys* species.

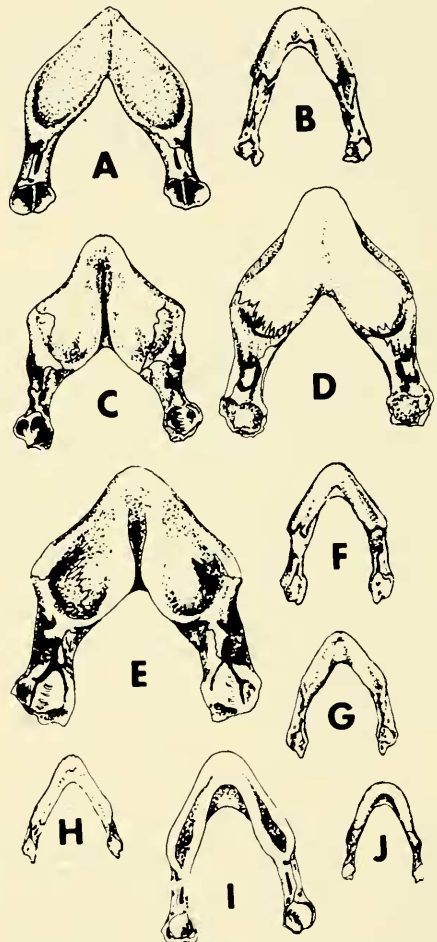


Figure 1. Shape of the symphyseal area of the lower jaw in mature females of (A) *Malaclemys terrapin*, (B) *Graptemys pseudogeographica*, (C) *G. geographica*, (D) *G. pulchra*, (E) *G. barbouri*, (F) *G. caglei*, (G) *G. versa*, (H) *G. ouachitensis sabinensis*, (I) *G. o. ouachitensis*, and (J) *G. flavimaculata* (the shape of the symphysis is the same for *flavimaculata*, *oculifera*, and *nigrinoda*).

(3) Bones surrounding the foramen palatinum posterius (Fig. 2). The bones surrounding that foramen in *Terrapene* and in the species of the *Pseudemys rubriventris* complex are the same as *Graptemys*; the other species of *Pseudemys* and the other N.A. emydid genera are like *Malaclemys*. Therefore, *Graptemys* and *Malaclemys* were possibly derived from different species of *Pseudemys*.

(4) The absence of contact between the ophisthotic and pterygoid due to the involvement of the exoccipital. If the condition in *Malaclemys* and *Deirochelys* represents a derived feature, this would strongly suggest that *Malaclemys* was not the ancestral stock from which *Graptemys* evolved. It could also indicate that a *Graptemys*, *Deirochelys*, or any other species of North American emydid turtle could have been ancestral to *Malaclemys*.

(5) The lack of a notch in the premaxillary bones. The lack of a notch in those bones in *Graptemys* and the presence of a notch in *Malaclemys* and the rest of the N.A. emyids, precludes determination of the possible ancestor for *Graptemys* and *Malaclemys* based on this feature.

SHELL FEATURES

(6) Flaring of carapace. The presence of such in *Graptemys* and to varying degrees in all other N.A. emyids except *Malaclemys* and some *Terrapene*, may indicate that flaring is an ancestral feature. If so, the upturning of the carapace in the last two genera would be a derived feature. This implies that *Graptemys* did not come from a *Malaclemys* stock.

(7) Double notching of some peripherals. The double notching of some of the peripherals is found only in *Graptemys* and in some individuals of *Pseudemys scripta* and *P. concinna*. This could indicate that *Graptemys* was not ancestral to *Malaclemys* and that a *Pseudemys* species was ancestral to *Graptemys*.

(8 and 9) The keel and its associated bosses (Fig. 3). A number of reports have dealt with the extent and development of the keel in *Malaclemys*. The last vertebral

scute is variable with respect to keel development. Say (1825) reported that the last vertebral in *M. terrapin centrata* was unkeeled; Wied (1865) noted that all of the vertebrals of *M. t. pileata* have a well developed keel. The keel in *Malaclemys t. centrata* was stated by W.P. Hay (1904) "to be rather low and rounded," whereas it was "always well developed," in *M. t. macrospilota*. A keel is thus not always present on the last vertebral, and I have not observed the end of the keel (the fifth boss area) to extend more than four-fifths the length of the last vertebral scute. W.P. Hay's (1904) statement about the keel and bosses of *M. t. littoralis* was: "the first vertebral plate is raised on the middle line to form a broad, low carina; on the second plate the elevation is greater, and stands out as a smooth boss . . . ; the elevation on the third plate has the form of a hemispherical button with a well-marked constriction around the posterior half of the base . . . ; on the fourth plate the elevation is raised into a knob-like protuberance from a base which is constricted all around . . . ; the fifth vertebral plate is flat or with only a trace of an elevation." Thus Hay's statement suggests that four or five bosses are present on the keel in *Malaclemys*. This is not always the case. Auburn University Museum of Paleontology (AUMP) specimen 2179 has only three bosses, and its shell structures are normal.

Concerning the total number of bosses on the keel in *Graptemys pulchra*, Carr and Goin (1955) said, "the dorsal keel . . . comprises a boss on each of the first four centrals, . . . weak to nearly lacking on the first and completely lacking on the fifth." A boss on the fifth central (vertebral) is not lacking in *pulchra*. Although it is not prominent in *G. pulchra* or in any other species of *Graptemys*, a terminal boss can be detected in all species. Cagle (1954), p. 182, Fig. 11) illustrated a juvenile *G. flavimaculata* that had five bosses on the carapace. I have never examined any specimen of *Graptemys*, including *G. flavimaculata*, in which the

TABLE 1

Diagnostic Characteristics of *Graptemys* and *Malaclemys* and An Outgroup Comparison of Those Genera with the Other North American Emydid Genera. Each Feature is Designated As Either Ancestral (Primitive = P) or Advanced (Derived = D).

<i>Graptemys</i>	<i>Malaclemys</i>	Other N. A. Emydines and <i>Rhinoclemmys</i> , a Batagurine
1. Sutural contact of maxilla with quad-ratojugal lacking. (P?)	In contact. (D?)	Lacking in <i>Terrapene</i> , <i>Emydoidea</i> , <i>Clemmys</i> , <i>Deirochelys</i> , <i>Pseudemys scripta</i> , <i>Chrysemys</i> , <i>Rhinoclemmys</i> and in some <i>P. floridana</i> . (P?) In contact in <i>P. concinna</i> and in the members of the <i>P. rubriventris</i> complex. (D?)
2. Rounded-shaped symphyseal part of lower jaw. (D)	Symphysis pointed. (P)	Like <i>Malaclemys</i> . (P)
3. Foramen palatinum posterius bounded on mediolateral and outer lateral sides by palatine. (D)	Bounded on outer later side by maxilla. (P)	The members of the <i>P. rubriventris</i> complex, <i>Terrapene</i> , and <i>Clemmys</i> -like <i>Graptemys</i> . (D). (<i>Chrysemys</i> , <i>Pseudemys scripta</i> , <i>P. concinna</i> , <i>P. floridana</i> , <i>Emydoidea</i> , and <i>Rhinoclemmys</i> -like <i>Malaclemys</i> . (P)
4. Exoccipital not responsible for the separation of the opisthotic and pterygoid when the latter two are not in contact. (P)	Exoccipital responsible for the separation of the two bones. (D)	<i>Chrysemys</i> , <i>Pseudemys</i> , <i>Emydoidea</i> , <i>Terrapene</i> , <i>Clemmys</i> , and <i>Rhinoclemmys</i> -like <i>Graptemys</i> . (P) <i>Deirochelys</i> -like <i>Malaclemys</i> . (D)
5. Premaxillae without medial notch. (D)	With medial notch. (P)	Like <i>Malaclemys</i> . (P)
6. Hind edges of carapace flared but not curved upward. (P)	Fore, lateral and hind margins of carapace normally curled upward. (D)	Like <i>Graptemys</i> except for some <i>Terrapene</i> . (P)
7. Posterior ends of some peripherals emarginate with double notching on at least some of those peripherals in juveniles and some adults. (D)	Same as in <i>Graptemys</i> except none with double notching. (P)	Like <i>Malaclemys</i> except double notching in some <i>Pseudemys scripta</i> and some <i>P. concinna</i> . (P)
8. Carapace with a medial keel. (P) It normally reaches from anterior end of first vertebral scute to posterior end of fifth vertebral scute.	Carapace usually with medial keel. (P) It normally reaches from posterior end of first vertebral scute to approximately four-fifths of the length of the fifth vertebral scute.	A medial keel present in most <i>Terrapene</i> , in <i>Emydoidea</i> , most <i>Pseudemys</i> , in <i>Deirochelys</i> , in two species of <i>Clemmys</i> , and in some <i>Rhinoclemmys</i> . (P) A very slight keel is present in some <i>Chrysemys</i> .
9. Keel with 5 bosses. (D)	Keel with from 3-5 bosses. (D)	No bosses. (P)

1. I am at present following the separation of *Chrysemys* into *Chrysemys* and *Pseudemys* based on the recent paper by Vogt and McCoy (1980). I am not following their division of *Pseudemys* into the genera *Pseudemys* and *Trachemys*.

10. Ventrolateral sides of nuchal bone (costiform process normally absent) extend laterally to contact the midline side of the first peripheral bone. (P)
- Ventrolateral sides of nuchal bone (costiform process present) extend laterally to beyond the medial side of first peripheral bone (contact with second peripheral not unusual). (D)
- Not in contact with second peripheral in *Pseudemys*, *Clemmys*, *Rhinoclemmys*, *Terrapene*, and *Emydoidea*. In fact, contact is on medial side of first peripheral in the latter two genera. (P) Just makes contact with second peripheral in *Deirochelys*. (D) No costiform process in *Emydoidea*. Costiform process in some *Clemmys* and in some *Rhinoclemmys*. Costiform process in *Deirochelys*, *Pseudemys*, and *Terrapene*.
11. Posterolateral borders of the nuchal bone at the area of the pleural scute sulci are notched. (P)
- Not notched (except in one specimen). (D)
- Notched in all *Terrapene* and in most *Chrysemys*, *Pseudemys*, and *Clemmys*. (P) Not notched in most *Deirochelys* and in all *Emydoidea*. (D) Notched in some *Rhinoclemmys*.
12. That part of the anterior border of the first costal bone is extended outward and notched. (P)
- Border is straight and unnotched except in one specimen. (D)
- Same as in 11.
13. Lateral edges of nuchal bone overlapped broadly by first pleural scute. (D)
- Not overlapped or slightly overlapped by first pleural scute. (P)
- Broad overlap in *Pseudemys*. (D) Slight to broad overlap in *Terrapene*. Not overlapped or only slightly overlapped in *Deirochelys*, *Chrysemys*, *Clemmys*, and *Rhinoclemmys*. (P) No overlap in *Emydoidea*.
14. Anterolateral border of the first vertebral scute confined to nuchal bone. (D)
- Not always confined to nuchal bone. (P)
- Not confined to nuchal bone in *Emydoidea*, *Clemmys*, *Rhinoclemmys*; only rarely in *Deirochelys* and *Chrysemys*. (P) Confined to nuchal bone in *Pseudemys*. (D) May or may not be confined to nuchal bone in *Terrapene*.
15. Amount of nuchal scute underlap is small and distal width of nuchal scute underlap broader than length of nuchal scute underlap. (D)
- Same as in *Graptemys*. (D)
- Large amount of nuchal scute underlap in all N.A. emydid turtles, except in some *Rhinoclemmys*. Distal width smaller than length in all except some *Pseudemys* and *Terrapene*. (P)
16. Amount of nuchal scute overlap is small except in *G. geographica*. (D)
- Small amount of overlap (D)
- Large amount in *Pseudemys*, *Clemmys*, *Chrysemys*, *Emydoidea*, *Deirochelys*, and in some *Rhinoclemmys*. (P) Small amount of overlap in *Terrapene*. (D)
17. Eighth costal contacts the eighth neural but not the seventh neural (all of the *G. pulchra* examined from the Conecuh River in Alabama have lost the eighth neural; the contact between the eighth costal and the seventh neural is therefore an abnormal condition in that population of *G. pulchra*). (P)
- Contact of eighth costal with seventh and eighth neural bones. (D)
- With eighth neural in all except for some *Terrapene* (some of the latter have lost the eighth neural and thus contact is with seventh neural). (P) Derived for some *Terrapene*.

Table 1 continued on next page

18. Well developed lateral ridges on the undersides of the first and fifth costal bones. (D) Not well developed. (P) Like *Malaclemys*. (P)
19. Distal widths of the three widest costal bones $1 > 5 > 3$ or $1 > 3 > 5$. (P? or D?) Distal widths of three widest costal bones extremely variable but with costal 1 widest. Closest pattern to that for *Graptemys* was $1 > 3 > 5 > 6$ and that condition found in a single specimen. (P? or D?) Variable within all.
20. Scutes of carapace sculptured but not concentrically so. (P) Scutes of carapace concentrically sculptured. (D) Same as for *Graptemys* except for some Antillean *Pseudemys*, *Clemmys insculpta*, and some *Terrapene*. (P) No sculpturing in *Chrysemys*.
21. Carapace with pattern. (P) Carapace with pattern dissimilar to that of any *Graptemys*. (D) Same as in *Graptemys* except for *Clemmys guttata*. (P)
22. Bridge relatively wide. (P) Bridge relatively narrow. (D) Same as for *Graptemys*. (P)
23. Seventh marginal scute normally separated from abdominal scute by inguinal scute (except in some individual *G. pseudogeographica*). (P) Seventh marginal contacts abdominal scute. (D) Like *Graptemys*. (P)
24. Axillary and inguinal scutes not reduced in size or absent. (P) Axillary and inguinal scutes reduced in size or absent. (D) Like *Graptemys*. (P)
25. Typical plastral formula is gular < humeral < pectoral < abdominal > femoral < anal (89%). (P? or D?) Typical plastral formula is gular humeral < pectoral < abdominal > femoral < anal (76%). (P? or D?) Variable.
26. Among plastral scutes the abdominal longest in longitudinal dimensions 82% of cases; anal longest 18% of cases. (P? or D?) Among plastral scutes the abdominal longest in longitudinal dimensions 53% of the time; anal longest 47% of the time. (P? or D?) Variable.
27. Plastron of juveniles with generally an ornate plastral pattern (except in most *G. geographica* and in all *G. barbouri*) (P) Some individuals have dark spots as in *Malaclemys*. Ornate plastral pattern in juveniles of *Chrysemys*, most *Pseudemys*, most *Terrapene*, *Clemmys*, *Emydoidea*, and *Rhinoclemmys*. (P) No pattern in *Deirochelys*. (D) Patterns of none are like those of *Malaclemys* except some mature *Pseudemys* males have dark spots.
28. Head, neck and limbs striped. (P) Not striped but blotched or spotted. (D) Like *Graptemys* except some *Rhinoclemmys* have stripes and spots on the head. (P)
29. Diploid chromosome number of 50. (D) Primitive number is 50 for emydines. Same as in *Graptemys* except for *Rhinoclemmys* (52). Primitive number in batagurines may be 52.

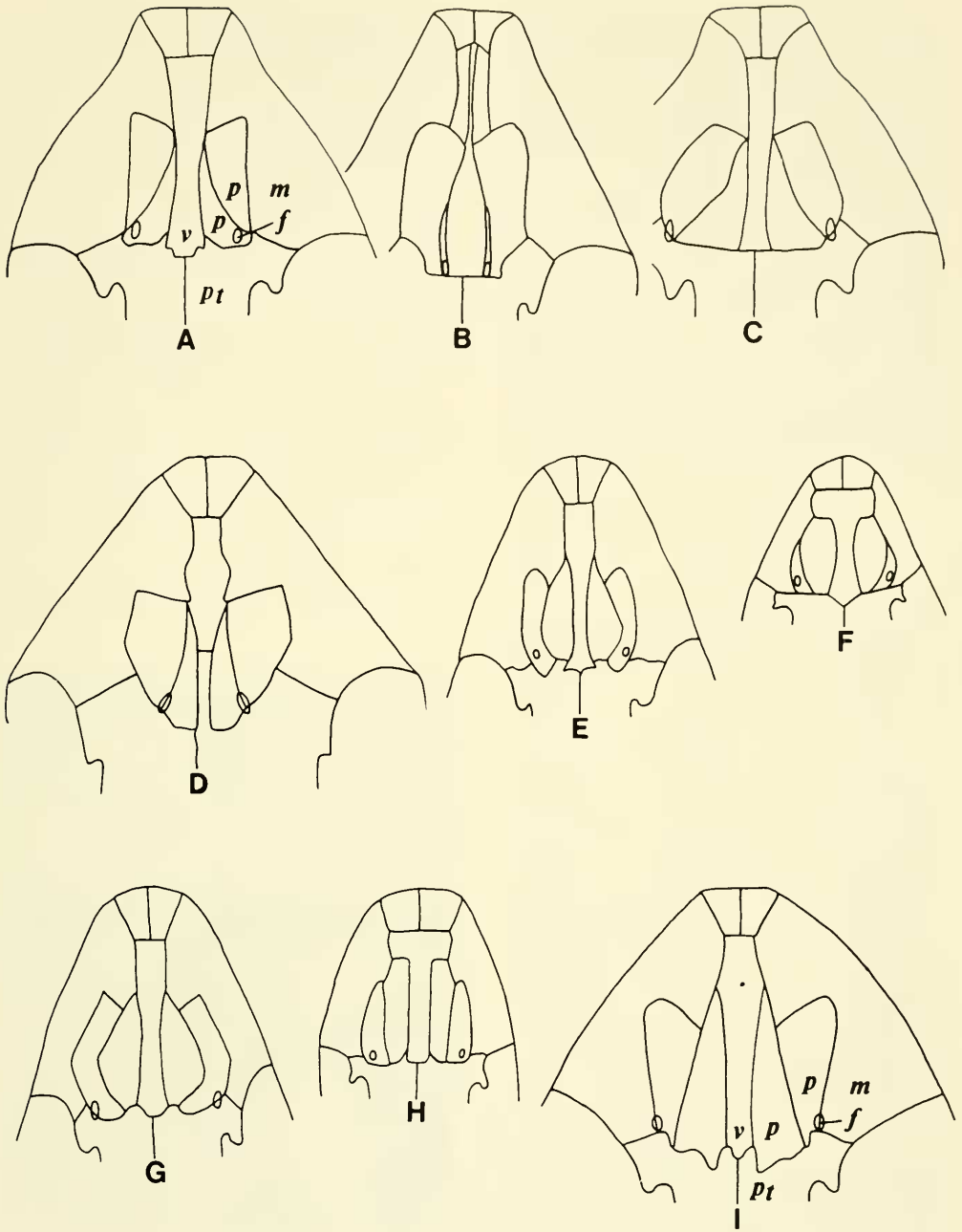


Figure 2. The location of the foramen palatinum posterius. The foramen is bounded on its mediolateral and outer lateral sides by the palatine in *Graptemys* (A) *pseudogeographica*, (B) *geographica*, (C) *pulchra*, (D) *barbouri*, (E) *caglei* and *versa*, (F) *o. sabinensis*, (G) *o. ouachitensis* and (H) *nigrinoda*, *oculifera*, and *flavimaculata*. It is bounded on its mediolateral and outer sides by the palatine and maxilla, respectively, in *Malaclemys terrapin* (I). Palatine (p). Maxilla (m). Foramen (f). Vomer (v). Pterygoid (pt).

fifth boss was located in the position illustrated by Cagle; the fifth boss is always at the posterior end of the last vertebral scute. The similar location of each boss in *Graptemys* and *Malaclemys* indicates their close relationship.

(10) Amount of ventrolateral extension of the nuchal bone and the costiform process of the nuchal bone. *Graptemys* normally lacks a costiform process; *Malaclemys* has one. Even though the nuchal of *Graptemys* is as wide as the same bone in *Malaclemys*, the distance the nuchal extends ventrolaterally is less in *Graptemys* than in *Malaclemys*. Therefore, the degree of such extension must not be solely a function of the width of the nuchal bone. This

seems to be the case since the distal width of the first peripheral is proportionately greater in *Graptemys* than in *Malaclemys*. Therefore, the presence of a narrower first peripheral and a costiform process in *Malaclemys* results in a greater ventrolateral extension of the nuchal in that genus than in *Graptemys*.

The other North American emydids that have a costiform process are *Pseudemys*, *Terrapene*, some *Clemmys* and *Deirochelys*, and the latter genus is the only group that has a ventrolateral extension similar to that of *Malaclemys*. I think it unlikely that *Deirochelys* was ancestral to *Malaclemys*; therefore, perhaps some *Pseudemys* turtle was the stock from which *Malaclemys* arose. The ancestral stock for *Graptemys* can not be determined with respect to this feature.

(11 and 12) The notching of the posterolateral borders of the nuchal bone and the anterior border of the costal bone (Figs. 4 and 5). The presence of such notching in *Graptemys*, *Terrapene* and in most *Clemmys* (14 of 16), *Pseudemys* (29 of 31), and *Chrysemys* (15 of 20), and not in *Malaclemys* (except in one specimen), *Emydoidea*, and most *Deirochelys* suggests that *Malaclemys* was not ancestral to

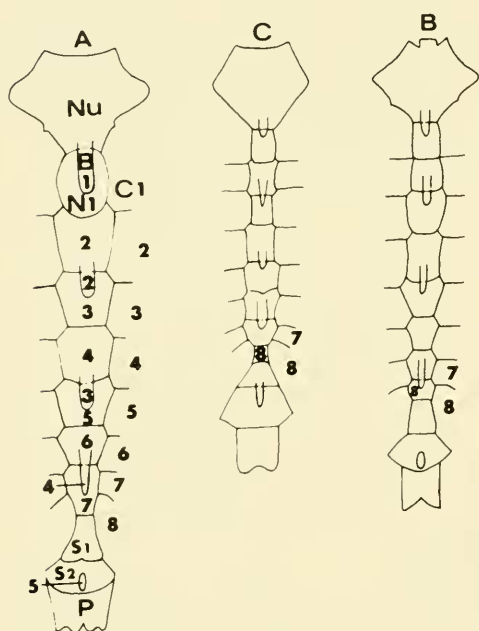


Figure 3. The location of the bosses in *Graptemys* (A) *pulchra*, (B) *nigrinoda*, and (C) *Malaclemys terrapin* and the contact of the eighth costal with the seventh neural in some *G. pulchra* due to the loss of the eighth neural bone. The normal contact is between eighth costal and eighth neural in *Graptemys* and eighth costal and seventh and eighth neurals in *Malaclemys*. Nuchal bone (Nu). Bosses (B 1-5). Neural bones (N 1-8). Suprapygal bones (S 1-2). Pygal bone (P). Costal bones (C 1-8).



Figure 4. Dorsal view of the nuchal bone in *Graptemys* (A) *pseudogeographica*, (B) *pulchra* and (C and D) *Malaclemys terrapin*. Arrows indicate notches. The position of the anteromedial edge of the first pleural scute and the anterolateral borders of the first vertebral scute are not on the nuchal bone in some *Malaclemys* (D).

Graptemys if the absence of notching is a derived feature. However, *Graptemys* could have given rise to *Malaclemys*, as could have *Clemmys*, *Chrysemys*, *Pseudemys*, *Terrapene*, *Emydoidea*, and *Deirochelys*. *Emydoidea* and *Deirochelys* presumably would be the best candidates from which to derive *Malaclemys* if relationships are based on the presence of shared derived features. In spite of the presence of a shared derived feature between those genera and *Malaclemys*, I do not believe that either one is a good candidate for being the progenitor of *Malaclemys*. Therefore, *Graptemys*, *Pseudemys*, and *Chrysemys* are considered to be more likely candidates. (13 and 14) The amount of pleural scute overlap on the nuchal bone and first vertebral scute - nuchal bone relationships. A great deal of pleural scute overlap exists in *Graptemys*, *Pseudemys*, and

in some *Terrapene* and the pleural scute always contacts the margin of the first vertebral scute on the nuchal bone in the first two of the three above (Dobie and Jackson, 1979). *Malaclemys* resembles most *Chrysemys* and some *Terrapene*, *Clemmys*, and *Deirochelys* in that there is little overlap of the pleural scute on the nuchal and the pleural scute does not always contact the first vertebral scute on the nuchal bone (Dobie and Jackson, 1979).

Malaclemys terrapin could have evolved from *Chrysemys* in which the extent of pleural scute overlap was minimal and the margin of the first vertebral scute did not always meet the pleural scute on the nuchal bone. If *M. terrapin* evolved from any species of *Graptemys* or *Pseudemys* that had a large amount of pleural scute overlap and contact between the two scutes on the nuchal bone, then presumably a reduction in the amount of pleural scute overlap must have occurred. *Graptemys* could have arisen from a *Pseudemys* stock.

(15 and 16) Amount of nuchal scute overlap and underlap and the width-length relationships of the underlap part of the nuchal scute (Figs. 6 and 7). The amount of nuchal scute overlap is small in *Malaclemys*, in some *Terrapene*, and in all extant species of *Graptemys*, except *G. geographica* (Dobie and Jackson, 1979). Both *Malaclemys* and *Graptemys* have smaller amounts of nuchal scute underlap than any other North American emydid turtle, and the distal width of the underlap part of the nuchal scute is broader than its length in both of those genera and in some *Pseudemys* and *Terrapene* (Dobie and Jackson, 1979). Based on these features, *Malaclemys* would seem to be more closely related to *Graptemys* than to any other extant North American emydid genus.

(17) Contact of the eighth costal bone with the seventh and eighth neurals (Fig. 3). The presence of such contacts in *Malaclemys* and the contact of the eighth costal with only the eighth neural in *Graptemys*



Figure 5. Dorsal view of the first left costal bone in *Graptemys* (A) *pseudogeographica*, (B) *pulchra* and (C and D) *Malaclemys terrapin*. That part of the anterior border of the costal bone that would adjoin the nuchal generally is straight and unnotched in *Malaclemys* as in (D). Arrows indicate notches.

(except for a single population of *G. pulchra*) and in all other North American emydid genera except *Terrapene* (the eighth neural is absent in some *Terrapene*) indicates that contact with the seventh neural is a derived character. The stock from which *Malaclemys* was derived presumably could have been any genus of North American emydid turtles; *Graptemys* could have come from *Pseudemys* or from any other North American emydid genus except *Malaclemys*.

(18) Lateral ridges on undersides of first and fifth costals (Fig. 8). The lateral ridges extending toward the midline of the carapace from the anterior and posterior ends of the bridge are well developed in *Graptemys* in contrast to those of *Malaclemys* and the rest of the North American emydid genera. The functional sig-

nificance of those ridges is not known but they may serve as supportive units for the carapace. *Malaclemys* and *Graptemys* presumably could have been derived from any one of those genera.

(19) Distal widths of the three widest costal bones. An attempt to indicate the degree of relationships of *Malaclemys* to any other emydid genus on the basis of this character would be impractical because of the extremely variable nature of the widths of the costal bones. The fairly consistent widths in the species of *Graptemys* does indicate that they are closely related.

(20) Sculpturing on the carapace. The sculpturing on the carapacial bones in *Graptemys* is similar to that of some species of *Pseudemys* (*P. floridana* and *P. concinna*) although the degree of sculp-

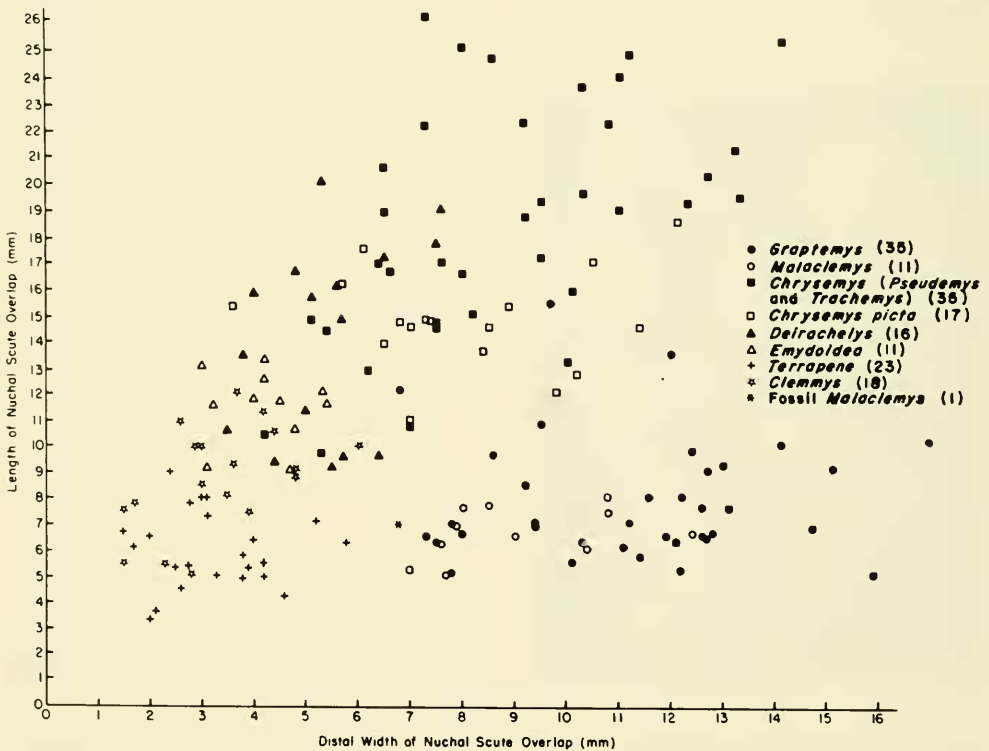


Figure 6. Length of nuchal scute overlaps versus distal width of nuchal scute overlap in various emydines including *Graptemys* (35) and *Malaclemys* (11).

turing in *Graptemys* is generally less than in any species of *Pseudemys* and more than that of *Chrysemys*. The type of concentric sculpturing in *Malaclemys* is unique and represents a derived feature (the species of *Terrapene*, some Antillean *Pseudemys*, and *Clemmys insculpta* also have concentric sculpturing (Zangerl, 1969; Dobie and Jackson, 1979) but the sculpturing patterns in the species of *Terrapene*, Antillean *Pseudemys*, and in *C. insculpta* are not the same as that demonstrated by *Malaclemys*. *Graptemys* may have arisen from *Pseudemys*; *Malaclemys* from any one of these genera including *Graptemys*.

(21) Carapacial pattern. The patterns on the carapace of the various *Graptemys* justify the name, "map turtle". Those patterns, although more similar to those patterns found in other North American emydids, except *Clemmys guttata*, are distinctive and were probably modified from a less elaborate carapacial pattern. The lack of similarity of the carapacial patterns of *Graptemys* and *Malaclemys* could mean that the patterns of both were independently derived from different an-

cestors or that they came from the same ancestor that had a less elaborate pattern. (22) Bridge width (Fig. 9). The width of the bridge in *Graptemys* resembles that of most aquatic emydids. The relatively narrow bridge in *M. terrapin* is distinctive, presumably derived, and perhaps is an adaptation for increasing the animal's ability for bottom walking in that a narrow bridge could allow the limbs to be advanced to a greater degree anteriorly than in a turtle having a wide bridge. *Malaclemys* could have come from any one of several different genera on the basis of this feature.

(23 and 24) The separation of the seventh marginal scute from the abdominal scute by the inguinal scute and the sizes of the inguinal and axillary scutes. The separation of the two scutes by the inguinal scute in *Graptemys* indicates that the size of the inguinal scute is about the same size as that found in most other North American emydids. The contact between the abdominal and seventh marginal scutes in *Malaclemys* is due to the small size of the inguinal scute or the absence of that scute. The condition in *Malaclemys* is probably derived.

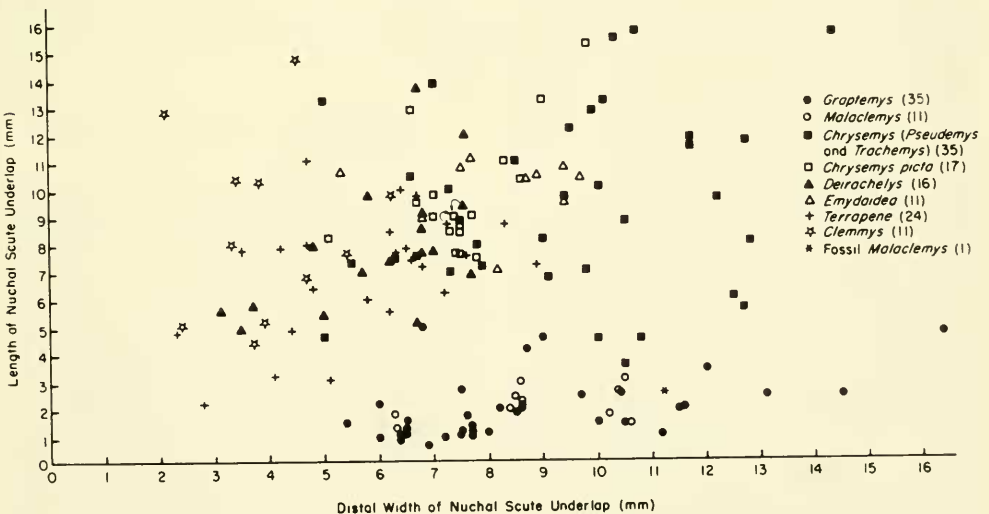


Figure 7. Length of nuchal scute underlap versus distal width of nuchal scute underlap in various emydines including *Graptemys* (35) and *Malaclemys* (11).

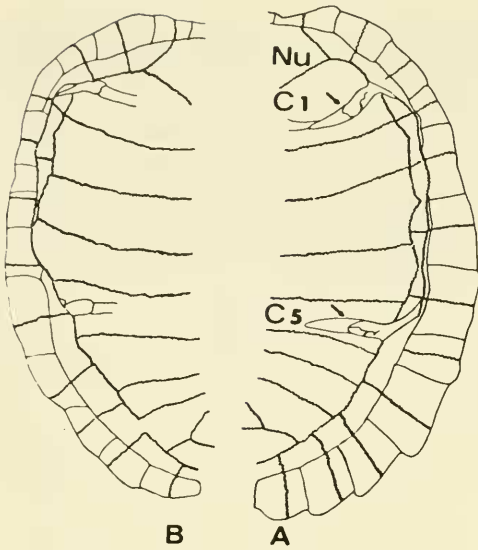


Figure 8. Lateral extensions of ridges on the ventral sides of the first and fifth costal bones in (A) *Graptemys nigrinoda* and (B) *Malaclemys terrapin*. The arrows indicate the ridges. Nuchal bone (Nu). Costal bone (C 1). Costal bone (C 5).

The size of the axillary scute in *Graptemys* is like that of most other emydids. It is either absent or very small in *Malaclemys*. The reduction in the size or loss of both the axillary and inguinal scutes is perhaps a result of the decrease in bridge width. Based on these features, *Graptemys* and *Pseudemys* are more similar than either is to *Malaclemys*.

(25 and 26) Plastral formulae and the length of the abdominal plastral scute. The two genera are more similar to each other in these two features than either is to any other North America emydid genus; they would thus appear to be closely related.

(27) Plastral patterns. The ancestral plastral pattern of *Graptemys* was probably ornate because to varying degrees ornate plastral patterns appear in all species of *Graptemys* except *G. barbouri*. The plastral patterns in *Malaclemys*, although ornate, do not resemble the pattern of any *Graptemys* species except for a single

specimen of *G. nigrinoda*. The ornate plastral patterns of both were probably derived from different ancestral stocks.

HEAD, NECK AND LIMB STRIPING

(28) Head, neck and limbs striped. The striping of such units is a typical emydid condition and *Graptemys* is no exception. According to Wood (1977), *Malaclemys* is striped although I and evidently Pritchard (1979) have never seen a striped individual and Ernst and Barbour (1972) use the absence of striping in *Malaclemys* as a feature in their key to U.S. turtles. If striping does occur in *Malaclemys*, it must be a rare condition. The absence of striping in *Malaclemys* is a derived feature. *Malaclemys* could have been derived from *Graptemys* or from any other North American emydid genus.

DIPLOID CHROMOSOME NUMBER

(29) Chromosome count. Because all emydines presumably have 50 chromosomes (Killebrew, 1977), *Graptemys* and *Malaclemys* could have been derived from each other, from any one of several different groups, or perhaps from a batagurine if in fact the 50 chromosome number of emydines is a derivation of the 52 chromosome number of the batagurines.

DISCUSSION AND CONCLUSION

All indications are that *Graptemys* represents a distinct group of closely related turtles. *Malaclemys* is undoubtedly more closely related to *Graptemys* than it is to any other extant genus, as would be evidenced by (1) the pterygoid forming a suture with the exoccipital except in some species of *Graptemys* (*G. nigrinoda* for example) and in some individuals of *M. terrapin*, (2) similarities in penial, pelvic girdle and hind limb morphology, (3) similarity in carapacial seam contacts (Tinkle, 1962), (4) similarity in the amount of nuchal scute underlap, and (5) similarity in the width-length relation-

ships of the underlap of the nuchal scute. In addition, the plastral scute formulae are the same for the two genera as are, generally, the locations of the bosses on the carapace.

The Oligocene species of *Graptemys*, *G. inornata* (Loomis, 1904) and *G. cordifera* (J. Clark, 1937) do not have shell characteristics that indicate a close relationship with *Malaclemys*. No other remains of *G. inornata* and *G. cordifera* are known. No fossils intermediate between *Graptemys* and *Malaclemys* are known, and only recently were fossil remains for *M. terrapin* discovered (Pleistocene age: South Carolina, [Dobie and Jackson, 1979]). Examination of an

Eocene specimen (South Dakota School of Mines and Technology, SDSM&T, 59187) identified as *Graptemys* by Bjork (1967), reveals that it is not *Graptemys* or *Malaclemys* because it lacks, among other things, a keel and bosses. The absence of the uniform fine granular tubercles on the external surface of the carapace of the Eocene fossil prevents its inclusion within *Compsemys* (a baenid turtle, Gaffney, 1972b) and the absence of a keel and rugosities rules out its inclusion within any genus of North American emydids except *Chrysemys* (some *Chrysemys* do have a slight keel). On the basis of the absence of the latter two features it is like *Chrysemys picta*. However, it cannot be

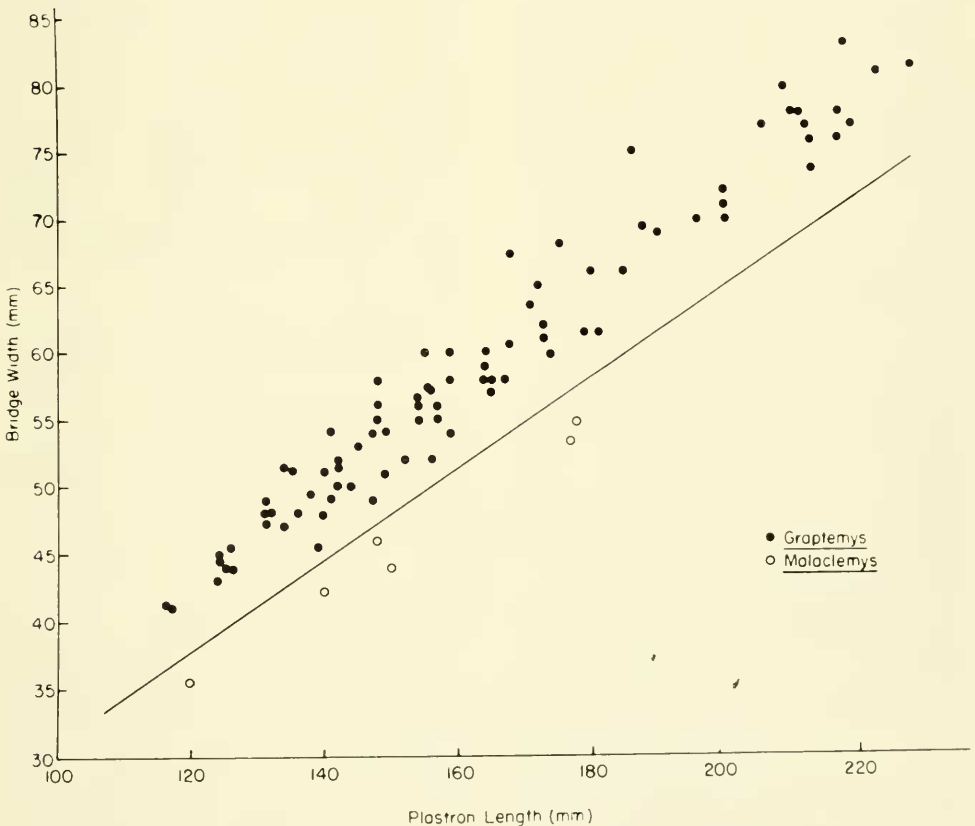


Figure 9. Relative bridge width in *Graptemys* and *Malaclemys*. The solid line depicts the separation of the two genera.

included within *Chrysemys picta* as the length of the sixth neural in *C. picta* is about twice as long as that of the fossil and the posterior width of the first suprapygial of the fossil is about twice the width of the same bone in *C. picta*. The neural bones of the fossil are narrow as compared to those of *Deirochelys carri*, *D. reticularia*, *Emydoidea blandingi*, *Malaclemys terrapin*, *Clemmys guttata*, and *C. insculpta* and this rules out the inclusion of the fossil into any of those genera.

The features possessed by the Eocene fossil do not fit those of *Graptemys*, *Malaclemys* or any extant North American emydine genus, thus, it may be a new taxon.

Although *Graptemys* and *Malaclemys* have several characteristics in common with some of the species of the Eocene emydine fossil turtles assigned to the genus *Echmatemys* (Table 2), I do not believe that either one of the two taxa nor any other new world emydine genus came from *Echmatemys*. O.P. Hay (1908) and Weaver and Rose (1967) proposed that *Chrysemys* came from *Echmatemys* and Hay (1908) also believed that *Echmatemys* was the ancestral stock for most other North American emydine genera. I reject the ancestral status of *Echmatemys* because to me many if not most of the species of *Echmatemys* appear to be members of *Rhinoclemmys* (e.g., McDowell, 1964, believed that *E. pusilla* belonged in the Neotropical batagurine genus *Rhinoclemmys*) and because most of the characters used to indicate relationships between *Echmatemys* and *Chrysemys* (in the sense of Weaver and Rose, 1967) were primitive characters and such can never be used to determine relationships. The *Graptemys* line may have arisen from some Eocene pre-*Pseudemys* of *Pseudemys* stock; *Malaclemys* may be an additional derivation of a *Pseudemys* stock or of a *Graptemys* stock, but its origin was probably somewhat later in the Tertiary (post-Miocene or later).

Loveridge and Williams (1957) believed

that *Graptemys* may have arisen from a *Pseudemys* stock, as did McDowell (1964), Ernst (1974), and Pritchard (1979), and that the ancestral *Malaclemys* was close to a *Graptemys* stock. The former is in disagreement with O.P. Hay's (1908) conclusion that *Graptemys* was from *Malaclemys*. Wood (1977) also considered *Graptemys* a *Malaclemys* derivative, and according to him, "most or all of these species evolved independently and perhaps also at different times during the latter part of the Pleistocene from *Malaclemys* rather than giving rise to one another." Assuming that each species of *Graptemys* was independently derived from *M. terrapin* as Wood believes, then each feature common to two or more *Graptemys* but absent in *M. terrapin* must exemplify convergence. A total of 24 features, at least 10 of which appear to be derived, are shared by all *Graptemys*, only six of these feature, at least three of which appear to be derived, are possessed by *Malaclemys*. It is highly unlikely that the remaining 18 features (seven derived and 11 ancestral) would have arisen independently in all *Graptemys* species.

Because of the number of features held in common by the species of *Graptemys* and because it is obvious to me and to other individuals (Cagle, 1952, 1953a, 1953b, 1954; McKown, 1972; Dundee, 1974; Killebrew, 1977; Vogt, 1978, 1980) that there are closely related complexes of *Graptemys* turtles, e.g., *G. nigrinoda*, *G. flavimaculata*, and *G. oculifera*; *G. pulchra* and *G. barbouri*; *G. pseudogeographica*, *G. ouachitensis*, *G. versa*, and *G. caglei*, (*G. geographica* belongs in a group by itself), I conclude that the various species of the *Graptemys* turtles were derived from other species of *Graptemys*. (The species of *Graptemys* are thus more closely related to each other than any one species is to *M. terrapin*.)

Wood (1977) apparently was unaware that there are two Oligocene fossil species of *Graptemys*. If the fossils are correctly assigned, the various species of *Grapt-*

TABLE 2

Characteristics of Various Genera of Emydine Turtles and of *Echmatemys*, a Genus that Presumably Has Members of the Batagurine Genus *Rhinoclemmys* Included Within It¹.

	<i>Graptemys</i>	<i>Malaclemys</i>	<i>Chrysemys</i>	<i>Pseudemys</i>	<i>Echmatemys</i>
1. Extensive overlaps of pleural scute on nuchal bone	+	-	-	+	-
2. Contact between first vertebral scute and pleural scutes always on nuchal bone	+	-	-	+	-
3. Extensive nuchal scute overlap on nuchal bone	±	-	+	+	+
4. Nuchal scute underlap short and length not exceeding its distal width	+	+	-	±	+
5. Inguinal scute normally separates the seventh marginal scute from the abdominal scute	+	-	+	+	+
6. Axillary and inguinal scutes always present and always relatively large	+	-	+	+	-
7. Premaxillae with medial notch	-	+	+	+	?
8. Exoccipital not responsible for the separation of opisthotic and pterygoid when the latter two bones are not in contact	+	-	+	+	?
9. Double notching on some peripherals	+	-	-	±	-
10. Eighth costal bone normally contacts only the eighth neural	+	-	+	+	+
11. Scutes of carapace sculptured but not concentrically so	+	-	+	+	+
12. Bridge width broad	+	-	+	+	+
13. Hind edges of carapace flared	+	-	+	+	+

¹The designations + and - indicate the presence or absence respectively of the feature.

emys obviously could not have been derived independently from *M. terrapin* during the Pleistocene.

Adult female *Malaclemys terrapin* and adult females of some species of *Graptemys* (*pseudogeographica*, *pulchra*, *barbouri* and *geographica*) resemble one another closely in general skull shape. The resemblance of *M. terrapin* to those *Graptemys* species is probably not due to common ancestry but rather to the development by each species of similar kinds of anatomical features (e.g., broad heads) as adaptations for feeding on similar kinds of food items (mussels.) *Graptemys pulchra*, *barbouri*, and *geographica* are also farther from the base of the *Graptemys* phylogenetic tree than is *G. pseudogeographica* (a species which is presumed to represent more nearly the ancestral-like stock) and both *G. geographica* and *G. barbouri* appear to be highly specialized, derived terminal end forms with respect to skull features. None of those species appears to be closely related to *Malaclemys terrapin* even though all have broad heads.

Mature females of some of the species of *Graptemys*, *G. nigrinoda*, *G. oculifera*, *G. flavimaculata*, *G. versa*, *G. caglei*, *G. ouachitensis* and some *G. pseudogeographica*, have narrow alveolar surfaces. The genus *Graptemys* cannot be differentiated, therefore, from *Malaclemys* on the basis of wide alveolar surfaces, as O.P. Hay (1908) contended.

The evidence is clearly against the lumping of *Graptemys* and *Malaclemys*. A subsequent paper will clarify the phylogenetic relationships of the *Graptemys* turtles.

ACKNOWLEDGMENTS

I am grateful to Drs. Robert Mount and George Folkerts for their advice on various aspects of this study. Several museums and one individual loaned me specimens and Robert Mount, John Pritchett and Lacy Hyche reviewed this manuscript. Theresa Rodriguez and Dr. Jeanne Stuart did most of the drawings.

SPECIMENS EXAMINED

Chrysemys picta: (74) (AUM 426, 605, 749, 829, 1170, 1553, 1915, 2062, 3827, 3872-73, 3875-76, 3884-85, 3999, 5669, 5885, 7072, 9514, 9747, 10091, 10126, 12587, 12589, 13616, 14133-34, 16231, 17366-67, 17871-72, 18033-34, 18218, 18812-14, 23478, 24109, 25088); (AUMP 132, 1713-23, 1965, 1967, 1983, 1985, 1990, 2117, 2171-76, 2318-20, 2351-54, 2405).

Clemmys guttata: (9) (AUM 21554, 22433, 26741, three classroom specimens); (AUMP 308, 2251); (UF/FSM 41018).

C. insculpta: (5) (AUM 29257); (AUMP 279); (UF/FSM 19016, 41525-26).

C. marmorata: (9) (AUMP 2260-62, 2264-66, 2310-11); (UF/FSM 41523).

C. muhlenbergi: (1) (UF/FSM 14116).

Deirochelys reticularia: (44) (AUM 1705, 1733, 3378, 3898, 8747-48, 9320, 10090, 10109, 10152, 11564, 12394, 13495, 15791, 18236, 18484, 18999, 19729, 22706, 22998, 23001); (AUMP 125-26, 897, 935, 1924, 2315, 2910); (UF/FSM T736, 6530, 7744, 14192, 14244-48, 30348, 34880, 35026, 38433, 40824, 41524, 41533).

Emydoidea blandingi: (17) (AUMP 1724-26, 1959, 1962, 1971, 2014-15, 2017, 2115, 2117, 2119, 2252-54, 2417-18).

Graptemys barbouri: (35) (AUM 3380-81, 5956, 6238, 6326-27, 6329, 6388, 6621, 8793, 8966, 9470-71, 9500, 9548, 9659, 10101, 10104-05, 10276, 11231, 12694-95, 13653-54, 14278, 21606, 22662); (AUMP 297, 325, 328-29, 931, 1733, 2357).

G. caglei: (10) (TNHC) 36066, 36071, 36084, 36088, 36093, 36097, 36103, 36621, 36627-28).

G. flavimaculata: (48) (AUM 5941, 5968-74, 6147, 6387, 8792, 8941-43, 8982-83, 9238-31, 9348, 9492-95, 9538-40, 9542-46, 10150-51, 10294, 10296-98, 13660-61, 23664); (AUMP 925, 940, 998-99, 2129, 2247).

G. geographica: (31) (AUM 5976-77, 6622, 9319, 9446-47, 10858, 11805, 11830, 12410-18, 12240-41, 13002, 21613, 22910, 23111, 23242, 29574); (AUMP 300, 909, 1940, 2355); (NLSC 622).

G. nigrinoda: (33) (AUM 5665, 5939, 5942, 5964, 5983, 5989, 8948, 8968, 8970, 9233, 9235, 9237, 9261-62, 9268, 10127, 10143-44, 10149, 10292, 10301, 12562, 12575, 12630, 12635, 21553, 22988-89); (AUMP 927, 1730, 2255-56, 2419).

G. oculifera: (23) (AUM 5951-53, 5979, 9333, 14289, 23665-69, 25136-39); (AUMP 304, 2125-28, 2215-16, 2248).

G. ouachitensis ouachitensis: (27) (AUM 9136-38, 25983-84, 25988, 26431-34, 26648); (AUMP 278, 309, 1738, 1997, 2131-32, 2136, 2200-04, 2273-75); (NLSC 9383).

G. ouachitensis sabinensis: (32) (AUM 24019, 24022-23, 24239-46, 24253-55, 25129-35); (AUMP 2121-24, 2244-46); (NLSC 10137-39, 10142).

G. pseudogeographica pseudogeographica: (24) (AUM 25985, 27090, 27101, 27113), (AUMP 2905, 2902, 2277-84); (SUSD 1520, 2855, 2860, 2862,

2880-83, two uncatalogued specimens).

G. pseudogeographica kohni: (81) (AUM 6843, 20715, 23985, 23989, 23991-97, 24020, 24191, 24224-25, 24247-52, 24259-60, 24263, 25989, 26385, 26401-02, 26406, 26422-25, 27093-98); (AUMP 305-08, 326-27, 2118, 2133-35, 2161-66, 2185-88, 2191-99, 2221, 2267-72, 2276, 2402, 2901); (KU 1183); (NLSC 2304, 5263).

G. pulchra: (37) (AUM 4997, 5000-01, 5004-06, 5597, 5742, 5961, 6302, 6311, 9467-69, 9532, 9535, 12556, 19898, 23482, 25140-44, 25977); (AUMP 301, 443, 926, 930, 936, 943-44, 989-91, 1000, 1960).

G. versa: (14) (AUM 16653, 22816, 23984, 24202, 24222, 26030-34, 29302); (AUMP 924, 2130 2137).

Malaclemys terrapin: (23) (AUM 8839, 14277, a classroom specimen); (AUMP 706, 932, 954, 963, 1732, 1734-37, 1956, 1980, 2157-58, 2179, 2403); (TU 15194, .2, 15195.1); (UF/FSM 22849a-49b).

Pseudemys alabamensis: (41) (AUM 4840, 9346, 9957, 10072, 11598-99, 11601-02, 11608, 11813-14, 12580, 12591, 16870-71, 17032-33, 19362, 26998, 27003-05, 27007, 27009-10, 27018, 27020, 27023); (AUMP 277, 298, 938, 1706, 1710, 1906, 2285, 2356, 2360-62); (USA 1501-02).

P. concinna: (142) (AUM 4560, 5901, 5994, 7432, 7567, 8918, 10140, 10147, 10396, 11294, 12650, 13553, 13639, 13743, 16906, 17139, 18483, 18975, 19140, 21802-05, 22825, 23248, 24201, 24208, 24214-16, 24223, 24227-28, 24280-81, 25126-28, 26413, 26416, 29298-01); (AUMP 17, 284, 288, 290, 311, 318-19, 693-94, 697, 881, 900-01, 911-12, 917-19, 933-34, 950, 1707-09, 1904-05, 1941, 1976, 1989, 1993, 2000, 2148, 2156, 2167-69, 2181-84, 2189-90, 2221 2286-90, 2292-94, 2316 2410-12); (FMNH 55646, 55649-52); (KU 33526); (SFA 2769, 2803, 2858, 2989, 3460); (TCWC 13735, 13965-67, 42345); (TNHC 536-37); (TU1637, 3605-06, 11940, 13464, 14414, 14421-22, .1-.3, .9-.10, 14441, .2-.3, .10, 14451, .2-.3, 14506.1, 14541, 16030); (UNM465, 30345).

P. floridana: (53) (AUM 1670, 7672, 8976, 9505, 9563, 10102, 10290-91, 10725-29, 11596, 12428, 12430, 12602, 13834, 17133-34, 19000, 19927-29, 21609, 21831, 22658, 23201, 23490, 23703, 27706, 27945); (AUMP 289, 440-42, 447-48, 700, 1703, 1712, 1727-29, 1902, 1948, 1963, 1981, 1998, 2249, 2291, 2309, 2404).

P. nelsoni: (19) (AMNH 80234); (AUM 27948); (AUMP 299, 446, 449, 913, 1702, 1946, 1964, 1982, 1992, 1994, 2200, 2413-16); (USNM 101393, 101398).

P. rubriventris: (25) (AMNH 69909-12, 77114, 77587, 77613, 99145); (AUMP 445, 2116, 2120); (CM 14022-29); (UF/FSM 1821 - six specimens).

P. scripta: (84) (AUM 3828, 6993-97, 7574-76, 7578-80, 11557-58, 11560, 13319, 21540, 24203, 24258, 24261-62, 24264-68, 25125, 27016); (AUMP 11.0-11.21, 12-15, 16.1-.5, 285-87, 317, 692, 1720, 1969-70, 1972-73, 1984, 1988, 1999, 2001, 2149, 2155, 2173, 2214, 2222-24, 2406-09).

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